

**Learning from the past to prepare for the future: Felids face continued threat
from declining prey richness**

Sandom, C. J.^{1*}, Faurby S.², Svenning J.-C.³, Burnham D.⁴, Dickman A.⁴, Hinks
A.E.⁴, Macdonald E.A.⁴, Ripple W.J.⁵, Williams J.⁴, & Macdonald, D.W.⁴

Affiliations

¹School of Life Sciences, University of Sussex, Brighton BN1 9QG

²Department of Biological and Environmental Sciences, University of Gothenburg,
Goteborg, Sweden

³Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus
University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark

⁴Wildlife Conservation Research Unit, Department of Zoology, Oxford University,
The Recanati-Kaplan Centre, Tubney House, Tubney, Oxon. OX13 5QL, UK

⁵Global Trophic Cascades Program, Department of Forest Ecosystems and Society,
Oregon State University, Corvallis, OR 97331, USA.

* Corresponding author

Orcid ID: 0000-0003-2294-1648

e-mail: C.Sandom@sussex.ac.uk

Abstract

Many contemporary species of large-felids (≥ 15 kg) feed upon prey that are endangered, raising concern that prey population declines (defaunation) will further threaten felids. We assess the threat that defaunation presents by investigating a late Quaternary (LQ), 'present-natural' counterfactual scenario. Our present-natural counterfactual is based on predicted ranges of mammals today in the absence of any impacts of modern humans (*Homo sapiens*) through time. Data from our present-natural counterfactual are used to understand firstly how megafauna extinction has impacted felid communities to date and secondly to quantify the threat to large-felid communities posed by further declines in prey richness in the future. Our purpose is to identify imminent risks to biodiversity conservation and their cascading consequences and, specifically, to indicate the importance of preserving prey diversity.

We pursue two lines of enquiry; first, we test whether the loss of prey species richness is a potential cause of large-felid extinction and range loss. Second, we explore what can be learnt from the large-scale large-mammal LQ losses, particularly in the Americas and Europe, to assess the threat any further decline in prey species presents to large-felids today, particularly in Africa and Asia.

Large-felid species richness was considerably greater under our present-natural counterfactual scenario compared to the current reality. In total, 86% of cells recorded at least one additional felid in our present-natural counterfactual, and up to 4-5 more large-felids in 10% of the cells. A significant positive correlation was recorded between the number of prey species lost and the number of large-felids lost from a cell. Extant felids most at risk include lion and Sunda clouded leopard, as well as leopard and cheetah in parts of their range. Our results draw attention to the continuation of a trend of megafauna decline that began with the emergence of hominins in the Pleistocene.

Introduction

Between ~100,000 and 1,000 years ago humans played an important role in the extinction of at least 166 large continental mammal species (≥ 10 kg) and the continental extirpation of a further 11 (Sandom et al. 2014). With the loss of aurochs (*Bos primigenius*) in 1627 (Tikhonov 2008), bluebuck (*Hippotragus leucophaeus*) in 1799 (IUCN 2008) and thylacine (*Thylacinus cynocephalus*) in 1936 (McKnight 2008, Ripple et al. 2015) amongst many others (IUCN 2013), it is clear that this anthropogenic extirpation of large mammals continues. The outlook for future mammal species is troubling, with 60% of large herbivores (≥ 100 kg) and 61% of large carnivores (≥ 15 kg) classified as threatened, vulnerable or worse, by the IUCN (Ripple et al. 2014, Ripple et al. 2015). The conservation of large mammals presents a particular set of challenges (Macdonald et al. 2014), and although there are numerous conservation success stories that are slowing this decline (Hoffmann et al. 2010), there is little prospect of completely stemming this long-standing tide of extinction.

Prioritising taxa for conservation is technically, operationally and ethically difficult. However, there are arguments that the conservation of large carnivores is important for ecosystem function (Ripple et al. 2014) and because they attract public attention through their charisma (Macdonald et al. 2015). Here, we focus on large-felids (≥ 15 kg) because they are hyper-carnivorous, highly endangered and make potent ambassadors for conservation (Macdonald et al. 2010). We use past relationships between prey and felid decline to assess the threat further declines in prey species (defaunation) pose to extant felids (Wolf and Ripple 2016). We do this by comparing and contrasting a Late Quaternary (LQ) ‘present-natural’ counterfactual (Peterken 1977) to the present reality. Counterfactuals are alternative scenarios to reality (e.g. Bull et al. 2014), which, in our case, could have occurred in the absence of modern human (*Homo sapiens*) intervention. Our present-natural counterfactual is based on the predicted ranges of mammals today in the absence of past and present human impacts, but taking climate change into account (Faurby and Svenning 2015). It is hypothetical representation of what present day felid distributions might look like, had modern humans not expanded out of Africa; for simplicity, we hereafter refer to this concept by the term ‘natural counterfactual’. We see this as a technical term unrelated to discussions of whether humans should be considered within or separate from nature.

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93 We use data from this natural counterfactual to understand firstly how megafauna
94 extinction impacted felid communities to date, and, secondly, to quantify the threat to
95 large-felid communities posed by further declines in prey richness in the future. Our
96 purpose is to use these scenarios to highlight the imminent risks that defaunation
97 poses to biodiversity conservation. Specifically, we highlight the importance of
98 preserving prey diversity to conserve charismatic large carnivores.

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100 The cause of predator decline in the LQ has largely been considered in the context of
101 the wider debate around the causes of the megafauna extinction. Thus, the primary
102 driver(s) of large mammalian predator extinction specifically remain unclear
103 (Barnosky et al. 2004, Koch and Barnosky 2006). With predator richness closely tied
104 to prey richness in a bottom-up direction at macro-scales (Sandom et al. 2013,
105 Sandom et al. in press), the loss of prey diversity may partly account for the extinction
106 of large carnivores, as postulated by Krantz (1970). However, in the opposite
107 direction, the role of predators as a cause of large herbivore extinction has also been
108 discussed. Ripple and Van Valkenburgh (2010) hypothesise that large carnivores
109 could have driven extinction through top-down pressure when combined with human
110 hunting. Alternatively, the loss of top-predators, through, for example, direct
111 persecution by humans, could have allowed stronger competitors amongst their prey
112 to dominate in the absence of their predators and exclude weaker competitors (Paine
113 1966). These hypotheses are not mutually exclusive; the arrival of modern humans to
114 rich large-carnivore communities increased top-down trophic pressures that may have
115 triggered the decline of large prey, the decline in prey availability and richness could
116 then have driven the decline in large carnivores, altering herbivore community
117 dynamics with potentially further cascading implications through the ecosystem
118 (Estes et al. 2011, Owen-Smith 1987).

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120 Evidence for large carnivores being driven extinct as a result of the loss of prey
121 availability has been generated by the use of population simulation models directed at
122 determining whether modern humans could drive the megafauna extinct by over-
123 hunting (Koch and Barnosky 2006). Models that specified modern humans as
124 megafauna hunting specialists indicated that they were not capable of driving
125 megafauna extinct because human population density was tied to a boom and bust

cycle dependent on megafauna density (Koch and Barnosky 2006). However, more realistic models, that specify humans as generalist omnivores, capable of maintaining high population density at low megafauna density by switching to alternative smaller prey and other food, did indicate humans could drive megafauna extinct. The latter models successfully predicted the extirpation of megafauna in North America with 78% accuracy (Alroy 2001). While humans are adaptable and generalist omnivores, large-felids are typically hyper-carnivores and are energetically constrained to predate primarily on large prey (Carbone et al. 1999). For example, the fossil record indicates that sabertooth cats did sometimes predate the largest prey available, proboscideans, albeit their young (Marean and Ehrhardt 1995, Palmqvist et al. 2003, Ripple and Van Valkenburgh 2010), and isotopic evidence suggests these felids preyed on a variety of large herbivores (Bocherens 2015, Coltrain et al. 2004). Therefore, models designed to depict humans as megafauna specialists (e.g. Koch and Barnosky 2006) may better reflect predation by large-felids that are more restricted to large-bodied prey. If so, these models may explain why the large-felids could co-exist with the megafauna prior to human arrival, and explain why they would, in turn, be susceptible to extinction in the face of large herbivore declines following the arrival of humans.

The number of large mammals lost between 132,000 and 1,000 years ago varies dramatically between biogeographic regions (Qian 2010; Fig. S1). The most severe losses occurred in the Nearctic, Neotropics, western Palearctic and Australian biogeographic regions, while in comparison, the Afrotropics and Indo-Malaya were minimally affected (Sandom et al. 2014). Because most large herbivores have already been lost in regions of high LQ extinction, most large herbivores and carnivores currently threatened today are in Africa and Asia (Ripple et al. 2014, Ripple et al. 2015). Here, we pursue two lines of enquiry; firstly, we test whether the loss of prey species richness is a potential cause of large-felid extinction and range loss. Secondly, we explore what can be learnt from the large-scale large-mammal LQ losses, particularly in the Nearctic and western Palearctic, to assess the threat any further decline in prey species presents to large-felids today, particularly in the Afrotropics and Indo-Malaya. We compare and contrast macro-scale predator-prey richness relationships between the natural counterfactual and the present reality to infer how predator-prey species richness relationships may have been altered (Hemmer 2004, Morales and Giannini 2014). Finally, we use the relationship recorded between lost

prey and felid species richness to estimate the number of large-felids at risk of extinction as a result of declining prey resources today.

Methods

Species Distribution Data

To contrast the current reality with our present-natural counterfactual, we used two sets of mammal species distribution data. For the current distribution we used global species distribution maps for all terrestrial mammal species (IUCN 2013), however, to avoid zero inflated data Australia and Antarctica were excluded because they have no felids. For the natural counterfactual, mammal distributions were taken from Faurby & Svenning (2015), representing the distribution of each mammal as it could have been today in the absence of modern humans.

Current and counterfactual polygonal distribution maps were converted to rasters on a Behrmann projection (a cylindrical equal area projection) with a resolution of 2 degree equivalents at the equator (~220 km). A species was counted as present in a cell if any part of the cell was covered by the species' range polygon. Further, grid cells missing data and grid cells with <50% land area were excluded, resulting in 3250 cells in our analysis. All data handling and plotting was performed in the R statistical program, version 3.3.2 (R Core Development Team 2016), using the raster (Hijmans 2015), rgdal (Bivand et al. 2015), and maptools (Bivand and Lewin-Koh 2015) packages (see Sandom et al. 2013 for further details).

Felid Diet Data

Data on extant felids were taken from the felid diet database FelidDIET (Sandom et al. in press). Of the 10 large extant felids that primarily prey on mammals, nine (the exception being snow leopard *Panthera uncia*) are recorded to have larger ranges in the natural counterfactual than in the present, with cheetah recording the greatest difference with its current range covering 16% of its natural range. The felid diet data recorded in FelidDIET are based on the felid and prey extant ranges, but prey availability will be greater under the natural counterfactual. To correct for this, the dietary preferences and mass characteristics recorded in FelidDIET were used to predict each felid's primary prey in the natural counterfactual ranges of all mammals. The procedure followed the prey extrapolation method used in Sandom et al. (in

press), but using natural species' ranges for the felids and all other mammals (see supplementary methods for further details). We focus here on primary prey but we recognise the potential for felids to switch to secondary prey if available, seemingly as jaguar (*Panthera onca*) has done in response to the loss of larger prey species in its range (Hayward et al. 2016), which warrants further examination.

In the absence of empirical data, diet for the seven extinct large-felids was extrapolated from taxon substitutes using phylogenetically close relatives that have similar ecological traits. American lion (*Panthera atrox*) and the cave lion (*Panthera spelaea*) were considered functionally equivalent to the extant lion (*Panthera leo*) (Barnett et al. 2009), although the degree to which cave lion was social has been questioned (Bocherens 2015), also calling into question the sociality of American lion as well. Although the American cheetah (*Miracinonyx trumani*) was a closer relative of puma it was considered functionally equivalent to the extant cheetah (*Acinonyx jubatus*) (Donlan et al. 2006a) and so this was used. For these three species the taxon substitute's diet data were used to predict the mammals likely to be preyed upon their extinct functionally equivalent species following the extrapolation method in Sandom et al. (in press; see supplementary material). For the four sabertoothed cats (*Homotherium latidens*, *Homotherium serum*, *Smilodon fatalis*, *Smilodon populator*), the lion was selected as the closest functionally equivalent species because it is large and social, and isotopic analyses support these species preyed on similar species to American and cave lion, albeit with a considerable degree of individual variation in behaviour within and between species (Anton et al. 2005, Bocherens 2015, Coltrain et al. 2004). However, there must have been niche differences among these taxa to have allowed their long-term coexistence (Anton et al. 2005). An important factor here is whether these extinct felids were social or not, as sociality increases the range of prey body masses that can be taken (Van Valkenburgh et al. 2015). Van Valkenburgh et al. (2015) suggest that determining sociality from the fossil record is difficult if not impossible, although Antón (2013), Carbone et al. (2009) and McHorse et al. (2012) make the case for sociality in these extinct sabertooths, proposing that high competition in felid communities of the Late Pleistocene would promote group living. Certainly, group size is an important factor in determining which group of large predators successfully competes for a carcass in Africa (Cooper 1991), which drives the evolution of social behaviour, although clearly not all African extant felids are

social and smaller felids may be disrupted from social living by larger felids (Mosser et al. 2015).

The species recorded on each extinct felid's potential prey list were categorised according to likely importance based on the relationships observed between felid body mass and prey body mass in Sandom et al. (in press). For all extinct felids, the minimum and maximum mass categories for primary prey and secondary prey (diet Categories 1 and 2, for definitions see Sandom et al. (in press)) were multiplied by the proportion by which the extinct felid was larger than the taxon substitute, to give a best estimate of primary and secondary prey (see supplementary material for sensitivity analysis). The predicted prey species of all large-felids under the natural counterfactual are recorded in Appendix 1, where Category 1 = primary prey, 2 = secondary prey, 3 = occasional prey, and 4 = non-prey. Finally, extinct potential prey species, that are likely to have been excluded as prey by this approach because they do not have close living relatives, were added to a felid's primary diet if that species was of the appropriate mass. Mammal body masses were derived from a previously compiled dataset (Faurby and Svenning 2016).

Data Analysis

Both felid and prey species richness were calculated per grid cell for the current and the natural counterfactual mammal distributions. Current prey species richness was calculated in two ways: 1) a species was counted if a felid that preyed upon this species was also present in the cell using the present reality distribution maps for prey and felids, 2) a prey species was counted if a felid that preyed upon this species was present in the cell using the felids' natural counterfactual distributions. The latter calculation of prey species richness provides an estimate of the loss of prey richness ignoring the decline in felid distribution and diversity. Generalised linear models (GLMs), with a poisson error distribution using a log link function, were used to test if prey species richness was a significant predictor of felid species richness in the present and the natural counterfactual structured by biogeographic realm which was included to account for the differing biogeographic histories in the different realms (Qian 2010; Fig. S1). To assess the degree of spatial autocorrelation, we computed correlograms of GLM model residuals using the 'ncf' package in R (Bjornstad 2012), with distance classes of 1000 km and used Spatial Autoregressive (SAR) models to

account for spatial autocorrelation.

The difference (as a percentage) in prey species richness between the natural counterfactual and present was calculated for each cell for each felid. These data were used to map whether the felids that lost the greatest proportion of prey species richness corresponded with the felids that were lost from the cell. The difference between the prey species richness in the natural counterfactual and the present was used to predict the difference in felid species richness, using a GLM, with a poisson error distribution using a log link function. This model was used to predict how many felids would be lost under a future scenario where all large-felid prey currently classified as vulnerable or worse by the IUCN (2013) were to go functionally extinct and thus no longer provide a viable prey resource.

We carried out two sensitivity analyses, firstly to determine the sensitivity of our results to the multiplication factor used to estimate the minimum and maximum primary prey masses of the extinct felids, and secondly, to determine the sensitivity of our results to removing *Homotherium latidens*, which is of uncertain presence in the LQ in the Palaearctic.

Results

Felid species richness was considerably greater under the natural counterfactual compared to the current reality, with 86% of cells recording at least one additional felid in the natural counterfactual (Fig. 1a,c,e). The Nearctic and Palearctic indicate the greatest difference between the large-felid communities of the two scenarios, with up to five fewer felids in the present reality (Fig. 1e). In the Nearctic, under the natural counterfactual, there were as many as six large-felids in some cells, and a community of five large-felids is predicted to have been typical across much of the western side of the region. This compares to just one large-felid in this region today, puma. In the western Palearctic, the natural counterfactual recorded at least four large-felids over much of the region, in comparison there is a maximum of one large-felid today, the Eurasian lynx (*Lynx lynx*). In Indo-Malaya, large-felid losses have been high in the west and east, while the community in the centre of Indo-Malaya remains relatively intact (with as many as 5 large felids; Fig. 1a,c,e). In the

Neotropics there is at least one fewer large-felid over 95% of the region now compared with the natural counterfactual (Fig. 1e). In the Afrotropics, the natural counterfactual records three large-felids over 88% of the region, whereas 20% of the region currently supports these three felid species (Fig. 1a,c).

Large-felid primary prey richness is highest in the eastern Afrotropics, eastern Indo-Malaya, western Neotropics in the current reality (Fig. 1b), as it was, together with most of the Neotropics, under the natural counterfactual (Fig. 1d). The southern Neotropics, small areas of southern and western Afrotropics, the Nearctic, and to a lesser extent European Palearctic, recorded the biggest differences in prey species richness between the two scenarios with the maximum difference being 59, 41, 40 and 21 respectively (Fig. 1f).

A significant positive correlation was recorded between prey and large-felid species richness, structured by bioregion, in both the natural counterfactual (Fig. 2; Table A1; $\chi^2 = 859.72$, D.F. = 9, $p < 0.001$) and current reality (Fig. 2; Table A2; $\chi^2 = 1770.5$, D.F. = 9, $p < 0.001$). For the natural counterfactual, the relationship was strongest in the Nearctic, where felid species richness was greatest, with a maximum of six felids in any one cell (Fig. 2). A strong relationship was also evident in the Palearctic (Fig. 2, Table A1). There is a correlation between prey species richness and felid species richness in all bioregions in the current reality (Fig. 2, Table A2). Spatial correlation was found to be minor (Fig. A2a,b), but to make sure that it did not bias our results, we also analysed the results using a SAR model and got similar results (Table A4 & A5).

In the Neotropics, Nearctic, and Palearctic, the felid species that have experienced the greatest loss of primary prey between the natural counterfactual and the current reality are the felids that were lost from the same cells, with 80% of cells recording a 100% match (Figs. 3 and 4). By contrast, only 17% of cells in the Afrotropics and Indo-Malaya lost the felids that lost the greatest proportion of their primary prey species between the current reality and the natural counterfactual (Figs. 3 and 4). The seven extinct large-felids experienced high prey species losses between the natural counterfactual to the present reality over their entire ranges, except for *Panthera*

spelaea that had some areas of minimal prey loss (Fig. 4), while all extant species had regions of their range that had comparatively low prey species richness losses (Fig. 4).

A significant positive correlation was recorded between the number of prey species lost and the number of large-felids lost from a cell, structured by bioregion (Table A3; $\chi^2 = 1381.4$, D.F. = 9, $p < 0.001$). The relationship was clearest in the Nearctic and Palearctic, but all regions indicated a positive correlation (Fig. 5). Spatial correlation was again found to be minor (Fig. A2c) and a SAR regression reported similar results (Table A6).

In the present reality, the primary prey species of large-felids are particularly threatened in eastern and central Afrotropics, Indo-Malaya, and western and central Neotropics (Fig. 6a). The model explaining the relationship between the number of prey species lost and the number of felids lost indicates that between one and five large-bodied felids are at risk in any one cell as a result of defaunaion (Fig. 6). The threat is particularly acute in Indo-Malaya, but also in East Africa and to a slightly lesser extent in the Neotropics (Fig. 6). The magnitude of the threat varies by biogeographic realm; losses are predicted to be most severe under the Palearctic relationship (Fig. 6e) and least severe under the Neotropics relationship (Fig. 6d).

If all currently threatened prey species become functionally unavailable for extant felids, then the two worst affected species would be the lion and Sunda clouded leopard (*Neofelis diardi*), which would, on average, lose 61% and 63% of their prey base respectively in each of their cells compared to currently available prey richness (Table 1; Fig. 4).

The sensitivity analyses indicate our results are robust to variation in the multiplication factor used to estimate extinct felid prey and the inclusion of *H. latidens* (Figs. A3 & A4).

Discussion

The counterfactual comparison of species richness points to a severe impoverishment of large-felid communities between the current reality and the natural counterfactual,

and confirms this is likely to get worse under a business-as-usual scenario. We predict that under a natural counterfactual there would be at least one additional large-felid over 86% of the world's continental terrestrial surface, excluding Australia and Antarctica, and up to 4-5 more large-felids over 10% of the area. Whether the loss of large-felids was primarily caused by direct or indirect conflict with modern humans is an important question in understanding part of the LQ megafauna extinction, and one to which the answer may shed light on the magnitude of current threats to large-felid communities. We find that only a small fraction (<41%) of the primary prey species available to extinct felids' under the natural counterfactual, would still be available in the current reality; in comparison, the prey base of the extant felids is relatively intact (Fig. 4, Table 1). The relationship between loss of prey species richness and the loss of felids also holds for extant lion, in terms of range contraction; millennia ago the lion lost large swathes of its range (Sommer and Benecke 2006) from which its prey has also been lost (Fig. 4), for example. Using these relationships recorded between the natural counterfactual and the current reality to project forward, the trend suggests large-felid communities are threatened everywhere. However, felids in Indo-Malaya and eastern Afrotropics are at particular risk in the future, as defaunation levels could match the levels already reached in the Palearctic, Nearctic, and Neotropics (Fig. 6).

Felid species richness, then and now, correlates with prey species richness, as might be expected, but the relationship differs between biogeographic realms. The relationship is particularly strong in the Nearctic where large-felid richness under the natural counterfactual is greatest. It is striking that in both the Nearctic and European-Palearctic, large-felid richness exceeds that of the Neo- and Afro-tropics, despite the higher primary prey species richness in these tropical regions (Fig. 1). This might be the result of earlier felid extinctions in the Afro-tropics. Low diversity in the Neotropical realm may reflect restricted dispersal opportunity from North America into South America, particularly for open-habitat species such as American lion, American cheetah and *Homotherium serum*. Alternatively, there may be a taphonomic bias between the regions. In the Afrotropics there is no evidence of *Homotherium* surviving beyond ~1.4 Ma (Werdelin and Lewis 2005), while a species of *Dinofelis* persisted until ca. 1 Ma (Werdelin and Lewis 2001), leaving a surprisingly limited large-felid community of three species. Furthermore, all three species are relatively small compared to those in the Nearctic and Palearctic, despite the high prey

availability for large-felids in the Afrotropics (Kitchener et al. 2010). Sabertoothed cats (Felidae: Machairodontinae) from three different tribes were found in the Afrotropics in the Plio-Pleistocene, creating a more diverse large-felid assemblage, but did not survive through to the Late Pleistocene, likely as a result of increased competition for prey with early hominins (Werdelin and Lewis 2013).

The natural counterfactual species ranges are estimates based on a number of assumptions, as described in Faurby and Svenning (2015). Extinct species ranges were typically based on fossil co-occurrences. As reported in Faurby and Svenning, this may lead to overestimates of species ranges. *Homotherium latidens*, amongst other the non-felid species that were included as potential prey in our analysis, is particularly noted as a species that may have an overestimated range. The validity of *H. latidens* presence in the region for this period has been debated (see Barnett 2014, McFarlane and Lundberg 2013), but a sample of *H. latidens* from the North Sea has been dated to ca. 28,000 BP, supporting its inclusion (Reumer et al. 2003). In either case, the very limited fossil evidence suggests *H. latidens* was exceedingly rare in the landscape, possibly as a result of a prolonged decline triggered by climate change, competition with other large predators and competition with hominins (Anton et al. 2005). Overestimations of species ranges would increase the diversity scores in those regions, with the potential of inflating the number of felids and prey lost between the two scenarios. However, our macroscale approach and the fact that our results are robust to the removal of *H. latidens* (Fig. A4) suggest that any overestimations of species natural range have a minimal impact on our results and conclusions.

Predicting the primary prey for extinct felids is challenging, but our estimates, which are conservatively broad and comparable to surviving felids (Table 5), clearly suggest that the extinct felids would have very few of their likely primary prey available today compared to surviving felids (Fig. 4). Johnson (2002) highlights that species of the family Felidae went extinct if they had low reproductive rates, and that this relationship is consistent with all mammalian families, suggesting the cause of extinction was consistent among mammalian families. Johnson (2002) also indicates that this extinction pattern across families is consistent with modern human causes, including increased direct exploitation or persecution of species or through competitive exclusion. Because large-felids are energetically constrained to prey upon

large species (Carbone et al. 1999), a reduction of, or reduced access to, large prey could cause a protracted decline and final extinction of large-felids. Our results, supported by large prey specialist predator-prey interaction modelling (Koch and Barnosky 2006), suggest that the decline and loss of large prey species as a result of the arrival of modern humans (Sandom et al. 2014) would have driven large-felids to extinction even without direct killing. There are a number of interesting examples from the fossil record that indicate large-predators can be susceptible to prey decline. For example, a recorded bottle-neck of the cave lion population has been linked to the decline in European bison, thought to be a primary prey species, ~ 50,000 years BP (Barnett et al. 2009). Other examples include, the extinction of a North American wolf ecomorph, thought to have been particularly specialised on megafauna, when other wolf populations survived (Leonard et al. 2007). California condors (*Gymnogyps californianus*) are now artificially fed livestock carcasses because of the loss of terrestrial and marine megafauna during and since the Late Pleistocene (Chamberlain et al. 2005). Other factors, such as direct conflict between modern humans and large-felids, would have exacerbated the problem.

Our results support the loss of prey diversity as a potentially important factor in the extirpation and continental extirpation of the largest felids in the Neotropics, Nearctic and Palearctic. Conversely, more recent felid range declines in the Afrotropics and Indo-Malaya are not occurring in the species that have lost the greatest proportion of their prey species (Fig. 3), and prey losses in general have been relatively modest in comparison (Fig. 4). Direct persecution and habitat loss have been important drivers of predator decline recently, and more and larger protected areas have been called for as part of the solution to preserving these species (Ripple et al. 2014). However, tracking forward, contemporary large-felids are likely to face an increasing threat from loss of prey species, even in protected areas (Lindsey et al. 2013). Our results suggest lion and Sunda clouded leopard could lose on average over 60% of their primary prey in each cell, comparable to the extinct American cheetah (Fig. 4). The Sunda clouded leopard appears to face as great a threat as did the extinct felids. However, diet data for this species are extremely limited and this might influence the results (Sandom et al. in press). While the risk prey loss presents to extant felids may not be quite as severe as that experienced by their extinct relatives from the Late Pleistocene (Fig. 4), extant felids face greater challenges from human-wildlife conflict

that are likely to be severely exacerbated by the loss of their wild prey. A particular concern is felids switching to prey on livestock because of the loss of their wild prey, which often leads to retaliatory killings (Kissui 2008). Furthermore, where prey richness and availability is declining together with habitat loss and fragmentation increased competition between felids will lead to greater pressure on smaller felids (Hayward and Kerley 2008).

If a lasting and secure future for these felids is to be found, it will be important to counter the threat posed by loss of their prey. From a large-felid perspective, further defaunation is a particularly pressing issue due to prey declines because of bushmeat hunting (Ripple et al. 2016). In Sarawak, Malaysia, 23,500 tons of bush meat are estimated to be consumed annually (Bennett 2002), while in Tanzania around 2,000 tons are confiscated annually, although understanding what these estimates mean in terms of defaunation rates is challenging (Lindsey et al. 2013). Interestingly, bush meat exploitation in South America is also a serious problem (Peres 2000), but is not predicted to impact South American felids as significantly because fewer large-felids' prey species are classified as threatened by the IUCN in this region (Fig. 6a). Where threatened prey species have or will become functionally extinct, it may lead to the loss of at least one big cat species in the foreseeable future and potentially entire felid communities (Fig. 5). Felids most at risk include lion, tiger, Sunda clouded leopard and regions of leopard (*Panthera pardus*) and cheetah ranges. The magnitude of the potential loss of primary prey species for tiger and lion is particularly alarming (Fig. 4), and our results draw attention to the continuation of an unhappy trend begun in the Pleistocene perhaps as much as two or more million years ago.

We present these relationships as speculations, intending to illustrate the principle that an understanding of the past can help in anticipating the future. If modern humans contributed to the demise of the primary prey of large felids, it follows that their impact would disadvantage these predators. Our point, therefore, is to emphasise that the emptying of the Late Pleistocene larder, attributable to modern humans, has reverberated through predator-prey systems to cause up to five fewer species of large felid today than would otherwise have been the case. Unfortunately, it seems continued losses of large prey are set to cause the loss of even more large felids in the future. Of course, insofar as direct persecution of these same felids may extinguish

497 them before they are starved out of existence, we should already be alerted to their
498 peril. Alternatively, this long-term perspective offers an opportunity to consider a
499 rewilded future where felids and their prey could be restored to their natural ranges. In
500 terms of restoring prey species to support felid conservation, even exotic species can
501 be viewed positively in the absence of native prey. For example, non-native wild boar
502 (*Sus scrofa*) in Brazilian Atlantic Forest are being seen as an important prey species
503 for recovering jaguar populations (Verdade et al. 2016). In terms of restoring felids,
504 the Eurasian lynx is re-colonising and has been reintroduced to lost range in Europe
505 (Linnell et al. 2009) and range expansion through reintroduction has been proposed
506 for tigers in Asia (Hebblewhite et al. 2014, Hebblewhite et al. 2012, Qin et al. 2015,
507 Wikramanayake et al. 2011), Eurasian lynx to the United Kingdom (Hetherington et
508 al. 2006), leopard to the Russian Far East (Hebblewhite et al. 2011), and lions and
509 cheetah as taxon-substitutes for the American lion and cheetah in North America
510 (Donlan et al. 2006b). These efforts may not only be important for species
511 conservation, but also to the functioning of ecosystems through the re-establishment
512 of trophic cascades (Estes et al. 2011). Data presented in this paper offer an important
513 resource for taking a systematic approach to exploring rewilding opportunities going
514 forward.

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Supplementary material ((Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.

Tables

Table 1: Average difference of prey richness per cell for each felid between the natural counterfactual, present reality and projected defaunated future.

Felid	Average percentage of prey lost from natural counterfactual to present (mean per cell)	Average percentage of prey lost from natural counterfactual to future loss of threatened prey (mean per cell)
<i>Panthera atrox</i>	84%	84%
<i>Panthera spelaea</i>	64%	64%
<i>Smilodon populator</i>	84%	91%
<i>Smilodon fatalis</i>	82%	82%
<i>Homotherium latidens</i>	75%	76%
<i>Homotherium serum</i>	78%	78%
<i>Panthera tigris</i>	28%	41%
<i>Panthera leo</i>	37%	61%
<i>Panthera onca</i>	17%	24%
<i>Miracinonyx trumani</i>	59%	59%
<i>Panthera pardus</i>	30%	40%
<i>Puma concolor</i>	23%	31%
<i>Acinonyx jubatus</i>	15%	43%
<i>Panthera uncia</i>	0%	11%
<i>Neofelis nebulosa</i>	14%	35%
<i>Neofelis diardi</i>	11%	63%
<i>Lynx lynx</i>	17%	30%

Table 2: Summary large-felid primary prey data. CF = Natural counterfactual.

Felid	Felid Mass (kg)	Max Prey Mass (kg)	Min Prey Mass (kg)	Felid Range Size Present (cells)	Felid Range Size CF (cells)	Total Mammal Richness in Range	No. of Primary Prey
<i>Panthera atrox</i>	433	1698.2	45	NA	319	545	37
<i>Panthera spelaea</i>	380	2943.2	43.8	NA	879	356	47
<i>Smilodon populator</i>	295	2000	32.2	NA	531	1483	72
<i>Smilodon fatalis</i>	219	1698.2	21.3	NA	350	552	40
<i>Homotherium latidens</i>	189	1417.5	22.5	NA	320	278	31
<i>Homotherium serum</i>	189	1587	21.3	NA	338	464	40
<i>Panthera tigris</i>	163	825	12	201	739	1249	51
<i>Panthera leo</i>	161	1417.5	15.0	339	877	1294	112
<i>Panthera onca</i>	100	62.4	1.2	402	631	1667	83
<i>Miracinonyx trumani</i>	88	372	3.4	NA	90	264	31
<i>Panthera pardus</i>	55	180.3	0.9	935	1663	2131	192
<i>Puma concolor</i>	52	420.1	0.3	749	998	1806	370
<i>Acinonyx jubatus</i>	47	213.5	1.6	183	1143	1410	105
<i>Panthera uncia</i>	44	130	3.3	216	216	578	12
<i>Neofelis nebulosa</i>	21	180.3	0.2	125	152	635	183

<i>Neofelis diardi</i>	21	180.3	0.8	58	68	413	59
<i>Lynx lynx</i>	18	180.2	1.5	849	1283	930	120

Figure Legends

Fig. 1: Maps of large-felid (≥ 15 kg) and primary, most important, felid prey species richness, comparing the present reality and a ‘natural’ scenario: (a) current felid species richness; (b) current felid primary prey species richness; (c) natural counterfactual felid species richness; (d) natural counterfactual felid primary prey species richness; (e) difference between natural counterfactual and current felid species richness; (f) difference between natural counterfactual and current felid primary prey species richness.

Fig. 2: Plot of the relationship between primary prey species richness and felid species richness in our natural counterfactual (left column) and the current reality (right column), across five biogeographic realms and collectively. Full statistical details are available in Tables A1 and A2.

Fig. 3: Map indicating whether the felids lost between the natural counterfactual and present reality were the felids that lost the greatest proportion of their prey, where 0 indicates none of the felids lost had lost the greatest proportion of their prey and 1 indicates all felids lost were the felids that had lost the greatest proportion of their prey.

Fig. 4: Proportion of the natural counterfactual prey species that are unavailable if prey species currently classified as threatened or worse by the IUCN become functionally unavailable if each felid occupied its predicted natural counterfactual range.

Fig. 5: Plots of the relationship between the number of primary prey species lost against the number of large-felid species lost between the natural counterfactual and the current reality. Black lines represent linear regression plots for each bioregion represented and collectively for all biogeographic realm. Full statistical details are available in Table A3.

Fig. 6: Maps predicting the number of felids threatened by defaunation: a) the number of primary large-felid prey species that are classified as vulnerable or worse by the IUCN, excluding data deficient species; b-e) the number of large-felids at risk per grid cell using the relationship reported between the number of prey species lost and the number of felids lost using the global relationship (b), the Nearctic (c), the Neotropics (d), the Palearctic (e).